21. A Comparative Study of the Buccal Glands and Teeth of the Opisthoglypha, and a Discussion on the Evolution of the Order from Aglypha *. By SUSHIL CH. SARKAR, F.Z.S.

[Received December 22, 1922 : Read March 20, 1923.]

(Text-figures 1–29.)

Introduction.

The comparative anatomy of the buccal glands, teeth, and the problem of the evolution of the opisthoglyphous Snakes forms the subject of this paper, and was suggested to me by Professor G. E. Nicholls, under whose supervision the investigation was begun in the Biological Department of King's College for Women, Household and Social Science Department. After the research had been in progress for three months Dr. Nicholls had to leave for Australia, and since then the work has been carried on under Miss Philippa C. Esdaile, D.Sc., F.Z.S. It is with pleasure that I acknowledge my indebtedness to Dr. Esdaile for her invaluable advice and criticism during the progress of the work.

I wish also to express my obligation to Professor Dendy and the Government Grant Committee of the Royal Society of London for a grant-in-aid. Lastly, I have to thank Miss Alfreda Newton for her kind assistance in cutting series of sections of a large number of heads of snakes, and also for taking photographs of specimens and sections.

Historical Facts.

The snakes chosen as types in this research belong to the Aglypha and Opisthoglypha, *i. e.* two of the three divisions of the Family Colubridæ. These differ from one another by the fact that in the Aglypha all the teeth in the maxilla are solid, whilst in the Opisthoglypha one or more grooved teeth are present in the posterior region. The members of the latter group are more or less poisonous.

The group Opisthoglypha is of special interest in that it is considered to be the connecting-link between the Aglypha on the one hand and the Viperidæ (with grooved teeth at the anterior end of the jaw) on the other; the group Proteroglypha is believed to have developed independently and directly from the former. Although the possible evolution of the Opisthoglypha was pointed out by Boulenger, no research to verify his statements has been attempted in connection with the important organs, such as the poison gland, its duct and poison fangs, taken concurrently. So far as I am aware, this is the first research on these lines.

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* Thesis submitted for Ph.D. degree, University of London, June 1922.

The presence of grooved teeth in the posterior region of the maxilla was first observed and discussed by Thomas Smith (**11**) and later by J. G. Fischer. In the year 1892, Niemann (**6**) published an account of the structure and relationships of the glands of the upper lip in general, but he described only three types of the Opisthoglypha. His work on this group is very scanty, while the diagrams are insufficient and wanting in detail, but the connection of the duct and the groove of the fang is well emphasized. In 1895, West (**15**) published a detailed description of the buccal glands and teeth of opisthoglyphous snakes. His paper made a considerable advance in the knowledge of this subject; his observations are still looked upon as a good groundwork, and his work is quoted by various authors. His descriptions, however, relate only to morphology. I have described four more genera of this group—*Chrysopelea*, *Tarbophis*, *Psammophis*, and *Cerberus*; the first two were not mentioned at all by West, and of the other two he gave only a short description of the teeth.

It was in 1896 that Boulenger put forward an account of the probable evolution of the Opisthoglypha from the Aglypha. He pointed out that in the higher genera of the Aglypha the series of teeth in the jaw shows an increase in size from in front backwards, so that we are gradually introduced to the opisthoglyphous condition, with a large fang in the posterior region of the jaw. In the higher types of both the Opisthoglypha and Proteroglypha this fang is always distinctly bigger than the tooth in front of it. Therefore in my discussions of the probable evolution of the fang of the Opisthoglypha from the somewhat enlarged posterior tooth of the Aglypha, I have selected those snakes in the Aglypha in which the posterior tooth is clearly larger than the preceding one—e. g., *Tropidonotus* and *Lycodon*.

Among recent papers on the Ophidia, those of Mary Phisalix are the most important. In her work (**9**) she discusses the accounts given by various authors, and she has attempted to arrange the members of this group in an ascending series on evolutionary lines, according to the disposition of the teeth. In this paper I have attempted a like task, but my series differs from hers in that I have tried to select for consideration only those Aglyphodont forms in which the last tooth has become markedly different from the rest. Also I have discussed what I consider to be the highest grade of evolution in the Aglypha—*i. e.*, the condition presented by those types in which the last tooth has acquired two cutting-edges instead of only one. Mary Phisalix does not continue her series beyond those with one cutting-edge. It should be noticed that my diagram of *Tropidonotus stolatus* (text-fig. 10) differs from hers (see p. 164, ref. 9).

The hinder tooth in my diagram of this species is represented as larger than the one in front of it. My observation is gathered from the dissection of several specimens.

Methods and Material.

Most of the snakes used for my observation were brought from India by myself. Some of them were preserved specimens, well fixed and suitable for histological purposes.

Unfortunately others which I had hoped to keep alive for physiological experiments had to be killed unexpectedly, and the tissues were only imperfectly fixed.

This investigation has necessitated the preparation and examination of a number of serial sections of the heads of snakes, and owing to the presence of the scales and hard bones forming the skull, this proved to be a difficult task. After many experiments the following method was successful.

The head was separated from the body close to the angle of the jaw, and placed in the fixing and decalcifying reagent aceto-bichromate (Bolles Lee, pp. 49 & 50). In order to ensure thorough penetration of the fluid, an incision in the scales was made just behind the eye, the lens of which was also removed. After a fortnight the head was taken out, and was carefully cut by means of a sharp razor into two halves by a median longitudinal vertical cut. Each half was again placed in fresh aceto-bichromate solution with the addition of one or two drops per 100 cc. of acetic acid. I found it necessary to leave it in this for three to four weeks to get complete decalcification. Each of the halves was then used for longitudinal or transverse sections. It was found necessary to leave the head in the paraffin bath at a low temperature for more than twelve hours. The sections were cut at a thickness of 10–15 μ. Several stains were tried, and I found the following most useful: Ehrlich hæmatoxylin counter stained with eosin or hæmalum and eosin. Each of these methods gave a good differentiation between the serous and the mucous secreting cells in the poison gland, the former being stained pinkish, the latter bluish. Both these being water stains, I found that the teeth and bone were often washed off the slide while being taken through the alcohol. To prevent this the slides were dipped in a thin solution of colloidin in 90 °/$_{\circ}$ alcohol. In order to verify my observations with regard to the duct and its connections with the fang, I made several cardboard models of portions of the jaw.

General Discussion on the Teeth in the Mandible and Maxilla and the Mechanism of the Hinged Teeth.

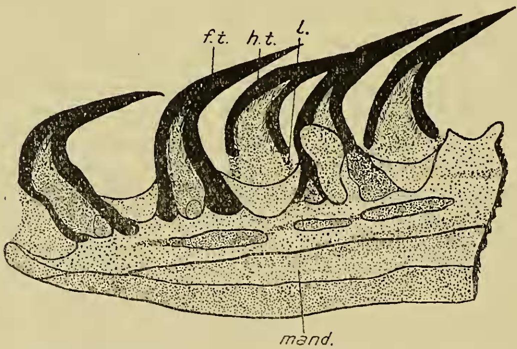
The maxilla, mandible, and pterygoid bear teeth and these occur in uninterrupted series, increasing or decreasing in size from in front backwards. Sometimes a diastema is left, and this is generally found in front of the tooth, which becomes bigger than the rest (*Dryophis*). The maxillary and mandibular teeth are mostly inclined posteriorly at a considerable angle—*i. e.*, the proximal part of each tooth for a little distance is almost at right angles to the bone, while the distal part bends backwards. The teeth appear to be of various types when seen in transverse section—round, triangular, flattened, etc. But more interesting still is the fact that the alternate teeth are hinged and fixed. In the dried specimens the hinged teeth frequently drop out; the dropping-out of the teeth after death has been frequently noticed by several workers, including Boulenger, and was accounted for by the accidents of preparation.

Thus, quoting Boulenger:—

> "It very often happens that every alternate tooth having dropped out, the jaw appears, on a superficial examination, to possess half the real number of teeth."

At first, while making dissections of a large number of snakes, I often found that some of their teeth differed from the others in that they could be bent backwards. I took it to be that these teeth were being either gradually fixed or were about to drop out of the jaw. On a more careful examination, I found that these loose teeth, as a general rule, alternate with the fixed ones. This regularity led me to suspect that the condition was not accidental. In order to verify this, I examined a number of cleaned skulls, and found that these loose teeth either drop out, leaving spaces or remain somehow fixed to the jaw, so that it is difficult to distinguish them from the fixed ones. I concluded from this that there must be some ligament or structure which

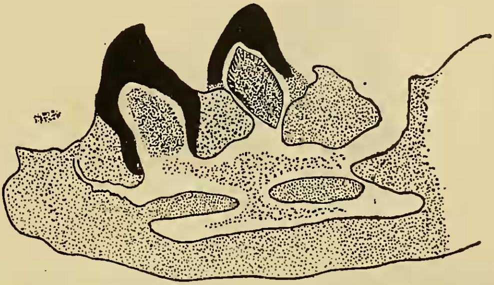
Text-figure 1.



Tropidonotus stolatus. Portion of mandible seen in lateral view, drawn with camera lucida from a cleaned specimen. *f.t.* fixed tooth; *h.t.* hinged tooth; *l.* ligament; *mand.* mandible. × 46.

keeps the tooth attached to the bone, but this hardens when dried, giving the tooth an appearance of being fixed. In order to make a further examination, I mounted the decalcified jaw complete, carefully dissected out from the head of the snake. In text-fig. 1 it will be seen that there are three fixed teeth, while the other two are attached to the socket by means of connective tissue (*l*), and there is a space, one tooth having dropped out during the process of dissection. I also cut sections of the heads of different genera, taking care to cut the jaw as nearly longitudinally as possible. Externally these hinged teeth differ from the others by being bent more sharply, and also, when moved with a needle, they can be made to bend towards the median line. As regards the forward movement, it is limited to a certain extent. At the base also the two sets of teeth differ from one another by the fact that the hinged teeth have a whitish appearance, due to the presence of the connective tissue which holds it to the bone. In order to study the mechanism of its movement, I carefully examined the series of sections of the tooth and the bone. Text-fig. 3 shows a diagram drawn from a longitudinal section taken at about the middle of the tooth. It will be noticed that the facets in the maxilla at the base of the two ends of the tooth differ in their structure, and, at the same time, the base of the tooth differs markedly at the anterior and posterior ends. In the front the base ends in a peculiar, slightly knob-like structure which also projects inwards. This fact was also noticed by Tomes (**13**), who writes as follows :—

Text-figure 2.



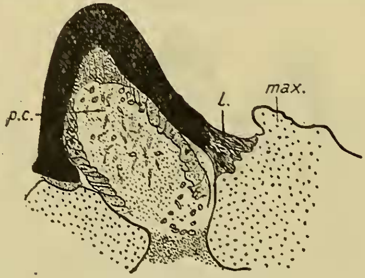
Tropidonotus stolatus. Longitudinal section of mandible with teeth. × 92.

> "As the tooth approaches completion, there is a peculiarity in the form which its base assumes and which I have not noticed in other animals, namely that the dentine at the widely open base of the tooth is often abruptly bent inwards as though the base of the tooth were about to be closed by a sort of operculum of dentine."

In his plate Tomes has given figures of sections of four or five teeth, and he has shown the bending in one only, and this also at the anterior side. This evidently proves that this was one of those hinged teeth.

This knob-like structure at the anterior edge of the tooth fits into the slightly concave, vertically inclined, smooth facet of the bone, so that when the tooth is pressed forward it strikes against the slightly inclined plane and is prevented from further bending. At the posterior side the distance between the bone and the end of the tooth is greater. The connective tissue between these two structures is more prominent, and its histological structure can be examined. Under the high power it has the appearance as shown in text-figs. 3 and 4, and it resembles white fibrous tissue. It has not at all the appearance of developing bone or enamel. Had it been enamel it would have been dissolved by the continued action of the acid in the decalcifying solution, to which it was subjected for more than a month. Text-fig. 4 shows also the connection of the same tooth at the posterior edge. It will be noticed that the connective tissue (*l*) keeps it attached to the bone. Thus we see that the tooth when pressed from in front moves so that the hinder end of the base, which has a greater field in which to move, is pressed down on to the bone; but it is prevented from slipping further by the connective tissue; while, on the other hand, if the tooth is pressed forwards from behind, its power of movement is restricted by the inclined edge of the socket of the bone and also by the band of connective tissue at the hinder end, which, so far as can be ascertained at present, appears to be non-elastic. This hinged and fixed arrangement I have found to be extended to the grooved teeth. If there are two grooved teeth, one of them is hinged and the other fixed. It depends upon the arrangement of the other teeth whether the anterior or the

Text-figure 3.

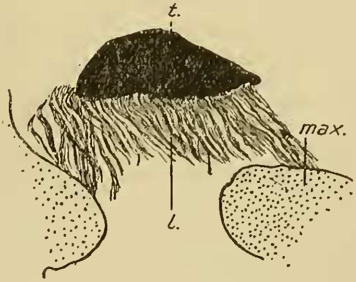


Tropidonotus stolatus. Longitudinal section of maxilla, showing a loose tooth with its connective-tissue attachment. *l.* ligament; *max.* maxilla; *p.c.* pulp cavity. × 260.

posterior one is hinged. It often happens that either the two or three consecutive teeth drop out from the dried bones. This is due to the fact that one of the fixed teeth is being replaced.

The function of such an arrangement is difficult to determine, but it seems to provide a firmer grip for the prey. While the prey is being taken into the mouth and forced towards the gullet, these hinged teeth, which point inward and backward, bend down; so that when the prey is struggling to escape from the mouth, the teeth, being hinged, allow it to pass downwards into the gullet but not outwards. Therefore from these observations I am led to conclude that the hinged teeth are not part of a series in the course of development which will become ankylosed to the jaw, but that they will always remain hinged, and during life will be held in place by the band of connective tissue, while after death they may drop out. This opinion is further emphasized by the facts that: firstly, in the maxillæ and mandibles of the dried skull of the adult we can clearly see the plane facets at the anterior end of the sockets, which show that it has been subjected to constant friction; secondly, if the tooth were to be later ankylosed to the jaw-bone, there would be no necessity for the inbending of the anterior end of its base; thirdly, it is inconceivable that in the numerous cases I have examined, every second tooth should become worn out or drop out accidentally.

Text-figure 4.



Tropidonotus stolatus. Longitudinal section of maxilla, showing a loose tooth with its connective-tissue attachment. *l.* ligament; *m.* maxilla; *t.* tooth. × 260.

The grooved fangs are always placed at the posterior end of the maxilla. Sometimes they are situated far back in the mouth, so that their points are quite hidden within the angle of the jaw. In this case the teeth are considerably bent (*Dipsas*), but where they are a little more forward in the mouth they are generally straighter. In shape they may be either flattened (*Oxybelis*) or circular (*Psammophis*), or may have a cutting-edge developed at the posterior region. The grooves are either placed in the front face of the tooth or on the external surface. In some cases the groove slightly curves round in its course; it may extend throughout the length of the tooth or may end a little above the tip. The groove may be shallow, or may be widely open or almost closed.

Morphological Description of the Dissection of the Heads of a few Opisthoglyphous Snakes.

Genus DRYOPHIS.

DRYOPHIS MYCTERIZANS. (Text-fig. 19.)

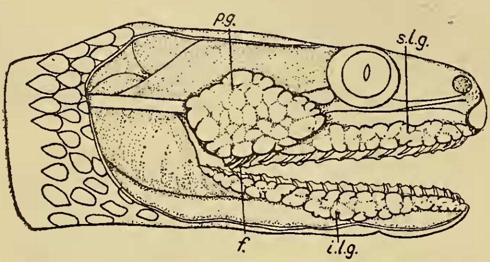
The poison gland is distinctly definable from the superior labial gland, and is large and extends a little further forward than the middle of the eye and posteriorly a little behind the angle of the jaw. The superior labial gland reaches to the anterior extremity of the maxilla, and it extends a little behind the poison gland. The two portions of the gland are continuous with one another. Near the region of the fang-like tooth in front the gland becomes broader. The inferior labial gland consists of a very thin strip of glandular tissue, and does not extend as far as the angle of the jaw. There are fourteen teeth altogether in the maxilla, and they are arranged as follows:—four small teeth in front, then two large fang-like teeth, followed by a diastema, then six very small teeth, and finally two very large, stout, and straight grooved teeth. The groove is on the outer side and is deep and extends throughout the length of the tooth. The duct of the poison gland opens near the base of the tooth. There are eighteen teeth in the mandible. The first is rather small, the next three very large, the middle of the three being the largest, then a diastema, which is followed by fourteen teeth which gradually diminish in size. The Harderian gland is much reduced, and consists of a thin strip of tissue lying behind the eyes in the eye-socket.

Genus CERBERUS.

CERBERUS RHYNCHOPS.

The poison gland is clearly distinguished from the upper labial gland, and is large and oval (text-fig. 5); it is so distinct an organ that it can be easily picked up from the surface of the superior labial gland without injury to the latter. The superior labial gland extends from the anterior end of the maxilla and posteriorly up to the poison gland. Practically the whole of the posterior portion of the glandular area is occupied by the poison gland, so that the superior labial gland does not extend far behind the eye. The lower labial gland also does not extend up to the angle of the jaw; this is probably due to the sharp upward turning which the lower jaw takes, thus giving a greater extension to the mouth and placing the fangs in a more exposed position. There are eighteen maxillary teeth; the last two are grooved and large. The grooved teeth are placed slightly further forward away from the angle of the jaw. The hinder grooved tooth is hinged. The groove is situated on the anterior side of the tooth at its proximal end, while on the outer side at the distal end. The groove does not extend up to the very end of the tooth, it is deep and almost takes the shape of a canal. The mandible contains twenty-two teeth of unequal size.

Text-figure 5.



Cerberus rhynchops. Dissection of head from the right side. *f.* fang; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *s.l.g.* superior labial gland. × 3.

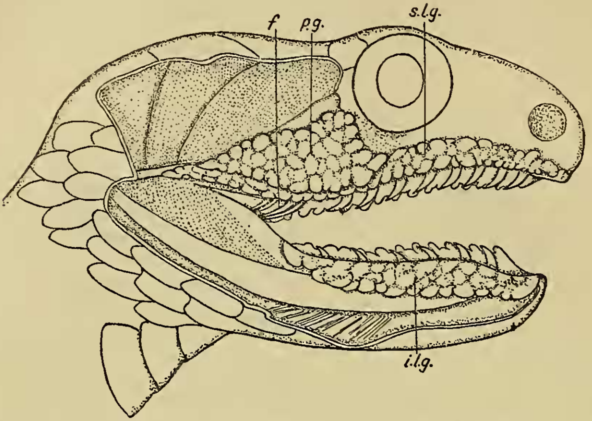
The Harderian gland is a little peculiar, for the greater part of the outer portion lies under the poison gland. There are three lobes; the external part is cylindrical, tapering at the posterior end, while the other two within the orbit divide into dorsal and ventral portions surrounding the optic nerve.

Genus Dipsas.

Dipsas trigonata.

The poison gland is clearly distinguishable from the superior labial gland, and anteriorly extends up to about the middle of the eye. The lobules of this gland are smaller than those of the superior labial gland and more distinct. The latter extends to the very end of the mouth anteriorly, and ends posteriorly about the angle of the jaw. It is continuous all along. The inferior labial gland is more highly developed than the superior labial gland, extending far back so that it almost meets the superior labial gland behind the angle of the jaw. The maxilla contains twelve teeth; the last two are grooved. The teeth are larger in front except the first one. The poison fangs are bent considerably backwards and slightly inwards so that the pointed ends are directed towards the pharynx. At the proximal end the grooves of the teeth lie on the outer side, while at the distal end they are in front of it, The grooves extend three-fourths the length of the tooth. The alternate teeth are hinged and fixed. The mandible contains about thirteen teeth; they are also larger in front, gradually diminishing behind. The

Text-figure 6.



Dipsas trigonata. Dissection of head from the right side. *f.* fang; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *s.l.g.* superior labial gland. × 3.

Harderian gland consists of three lobes, two within the orbit and the larger part outside.

Genus Chrysopelea.

Chrysopelea ornata. (Text-fig. 17.)

The poison gland is very small, smaller than in any opisthoglyphous snake I have examined, and it occupies a small area posterior to the eye. The smallness of the gland may be due to the huge growth of the eye. The superior labial gland is well developed, and extends posteriorly further than the angle of the jaw and anteriorly to the very end of the maxilla. The lobules of this gland are larger than those of the poison gland. The inferior labial gland is also fully developed, and is broader at the posterior side. The maxilla contains twenty teeth; the first three are very small, and they increase in size posteriorly; the last two are grooved. The groove is situated on the outer side and is widely open. It arises almost from the base of the tooth, and ends about one-eighth of the length of the tooth from the apex. In section the teeth are nearly oval in shape. The mandible contains twenty-two teeth: the first is very small; there is an increase in size up to the seventh, which is the largest, and then a gradual decrease. Both maxilla and mandible show the alternately fixed and hinged arrangement of teeth.

The Harderian gland consists of three lobes; two portions lie within the orbit and one outside.

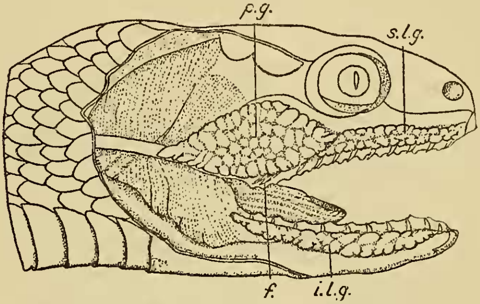
Genus TARBOPHIS.

TARBOPHIS VARIEGATUS.

The specimen of this snake was in a damaged condition.

The poison gland is large, and quite distinct from the superior labial gland; it is spindle-shaped, the anterior end lying below the middle of the eye. The superior labial gland is narrow, and reaches the anterior end of the maxilla, where it enlarges and curves round to join the gland of the other side. It is also continuous below the poison gland. The inferior labial gland extends from the very end of the mandible in front, and meets the superior labial gland posteriorly behind the angle of the jaw. Of the nine teeth in the maxilla the last is large and grooved, and the rest are smaller and subequal in size. The grooved tooth is situated far behind within the buccal cavity. The groove is placed on the external surface of the tooth, and does not extend up to the end of the tip. There are about fourteen teeth in the mandible, the series decreasing in size posteriorly. They are alternately hinged and fixed. The Harderian gland consists of two lobes, one outside and the other within the orbit, and it is perforated by the optic nerve.

Text-figure 7.



Tarbophis variegatus. Dissection of head from the right side. *f.* fang; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *s.l.g.* superior labial gland. × 3.

Genus PSAMMOPHIS.

PSAMMOPHIS SIBILANS. (Text-fig. 21.)

The poison gland of this specimen shows the most highly-developed condition among the opisthoglyphous snakes that I have examined; it is a distinct organ, and has assumed a definite shape, being oval. It is comparatively very large. The lobules of the gland are much smaller than those of the superior labial gland. The latter is continuous below the poison gland, and extends anteriorly to the very end of the snout, meeting its fellow of the other side. Behind it extends further back than the poison gland. The inferior labial gland is also well developed, and has the appearance of a compact body reaching as far as the end of the mandible, and posteriorly it meets the superior labial gland behind the angle of the jaw. The maxilla possesses four medium-sized teeth in front, then two large, solid fang-like teeth, followed by a series of four small equal teeth and finally two large straight fangs. The groove of the posterior maxillary teeth is placed on the anterior face of the tooth, and extends throughout the length of it, ending at the tip. The teeth in the maxilla and the mandible are straight and slightly directed backwards, and they also show an alternating arrangement of hinged and fixed teeth. The Harderian gland consists of two lobes, one outside and the other within the orbit. The latter shows a superficial division into two.

Discussion on the Evolution of the Opisthoglypha.

It is generally admitted that the opisthoglyphous snakes are evolved from the Glauconiidæ, and that the immediate ancestors of the Opisthoglypha are the Colubridæ Aglypha. Boulenger pointed out in the year 1896 (1) "that from Aglyphodont forms, in which the teeth increase in size posteriorly, we are gradually led to the Opisthoglypha, which are only to be distinguished by the presence of more or less deep grooves on the posterior fang-like teeth."

As far as my own observations go, I find that, apart from the gradual increase in the size of the teeth, there is a change concurrently in the structure of the particular tooth which is situated in the posterior portion of the maxilla near the opening of the duct of the parotid gland into the mouth. At the same time, the parotid gland itself undergoes a gradual transformation from a simple structure, distinguishable only from the superior labial gland by its colour, to a separate distinct organ lying detached from it. There also occurs a change in the connection of the duct of the parotid gland with the buccal cavity and the teeth.

My observations are based on a study of the following types, arranged in order:—

Dendrophis pictus. *Tropidonotus stolatus.* *Lycodon aulicus.*	} Aglypha.
Oxybelis fulgida. *Chrysopelea ornata.* *Dryophis mycterizans.* *Psammophis sibilans.*	} Opisthoglypha

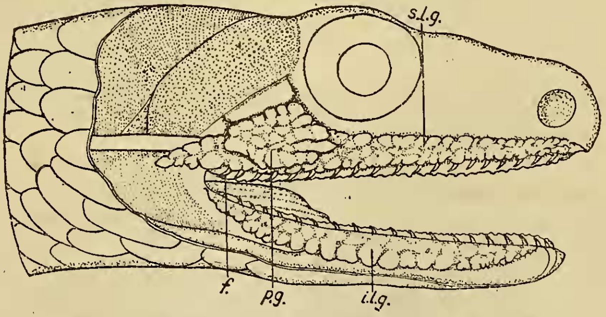
I had hoped to be able to obtain several specimens of both *Xenodon* and *Dispholidus*, in order that a full study might be made of the characters of the "poison apparatus" in these peculiar types. But in this I have been disappointed. I have made some dissections, but it was impossible to obtain a good set of serial sections. So I am unable to determine what further questions might be raised by such a study, or how a complete knowledge of the conditions exhibited by *Xenodon* and *Dispholidus* might affect the general lines of my arguments. However, I hope at some future date to work on these two genera, comparing and contrasting them with the genera I have had the opportunity of studying.

Aglypha.

DENDROPHIS PICTUS.

The anatomy of the general dissection of the glands and teeth of *Dendrophis* is shown in text-fig. 8. Of the two glands in the maxillary region the superior labial gland occupies the greater area, while the so-called parotid gland is confined to a small space. As will be seen, they are so intimately related that it would be difficult to distinguish one from the other but for the colour. This fact struck earlier workers too. Leydig (1873), in his work on *Tropidonotus*, described that the "superior maxillary gland divides itself into two portions which are distinct in the form and the colour of their follicles; the inferior part is grey and the principal part is of a yellowish colour, and the follicles are larger than on the grey part."

Text-figure 8.

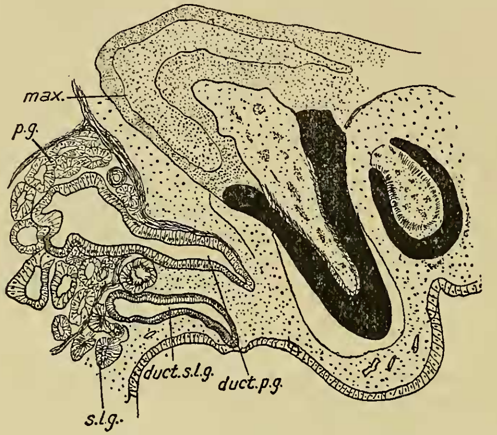


Dendrophis pictus. Dissection of head from the right side. Letters as before. × 3.

Evidently this yellowish portion becomes specialised to secrete a fluid different from that secreted by the rest of the gland; and we shall see later that this fluid becomes more and more important in the higher snakes as a weapon of defence, and that the teeth become modified to allow of its more careful use.

In the transverse section of *Dendrophis* (text-fig. 9) the superior labial and parotid glands and the ducts arising from them are figured. On comparing these ducts, it will be seen that the duct of the superior labial gland opens into the mouth at some distance from the round peg-like tooth and has no connection with it, while the duct of the parotid gland, formerly forming one of the series of the salivary ducts, has shifted its position in order that it may open nearer to the hinder tooth. In the maxilla there are about twenty teeth, small and almost equal in size; but the hinder tooth, referred to above, is bent backwards at a greater angle than the rest, also a slight cutting-edge has developed on the posterior face.

Text-figure 9.



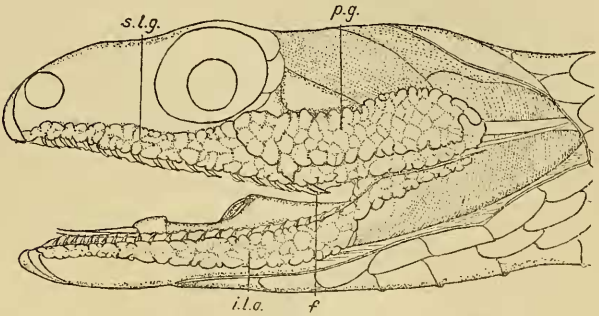
Dendrophis pictus. Transverse section of a portion of the head in the region of the superior labial and parotid glands, showing their ducts. Letters as before. × 63.

As in all other harmless Batrachians and Reptiles, the teeth are used to prevent the prey from slipping out of the mouth, and at the same time to make small punctures in the body while it is being killed by suffocation. Meanwhile the buccal cavity is flooded with the secretion from all the buccal glands, and the mixed saliva covers the animal and gradually finds its way into the small wounds made by the primitive round teeth.

TROPIDONOTUS STOLATUS.

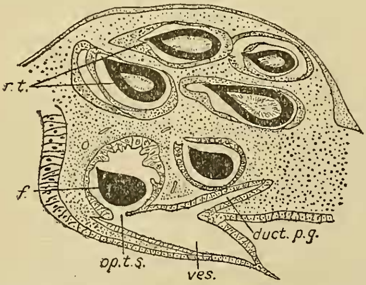
Text-fig. 10 shows the external features of the gland as seen after the removal of the skin, and also the maxillary teeth from the left side. It reveals a condition strangely advanced in some features, but on the whole distinctly similar to that of *Dendrophis* (text-fig. 8). Of the more highly-developed parts the parotid gland and the posterior tooth are most striking. The gland (*p.g.*) is quite well developed, and it extends far behind, as far as the angle of the jaw, and in front up to the middle of the eye, while in shape it is peculiar in being rectangular; in fact, as will be seen from the diagram (text-fig. 10), more than half the glandular area in the region of the maxilla has taken up the function of the secretion of the serous fluid. Apart from its great development in size, the dissection shows that the parotid gland is really a part of the superior labial gland, and is only to be distinguished from it by its yellow colour.

Text-figure 10.



Tropidonotus stolatus. Dissection of head from the left side. Letters as before. × 6.

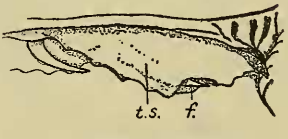
Text-figure 11.



Tropidonotus stolatus. Longitudinal section of the head in the region of the poison fang and duct of parotid gland. *f.* fang; *duct p.g.* duct of poison or parotid gland; *op.t.s.* opening of duct into tooth sac; *r.t.* reserve tooth; *ves.* vestibule. × 63.

The maxilla bears about eighteen teeth, these being subequal in size, except the last. This (*f*) is much increased in size, and is more than twice the length of the tooth in front of it. It is considerably bent backwards. But apart from its being distinguished from the others by its size, it is important to notice that it is separated from them by being enclosed in a special sac (text-fig. 12, *t.s.*) formed from the folding of the mucous membrane; in fact, it has all the external appearance of a fang contained in a tooth sac, and the similarity is so great that it can readily be mistaken for the fang of the poisonous snakes. Further, we can see from the portion of the longitudinal section of the head of *Tropidonotus* that the tooth is specialised by the growth of a cutting-edge on the posterior side. Besides, as in other poisonous snakes, there are reserve teeth (*r.t.*) lying on the inner side of this fang-like tooth. Text-fig. 11 shows the connection of the duct of the parotid gland with tooth and mouth-cavity. It is remarkable that the duct of this gland enlarges at first into a special sac, the vestibule (*ves.*), which is in communication with the tooth sac by an opening (*op.t.s.*). The vestibule opens into the buccal cavity (text-fig. 13, *op.d.p.g.*). Hence we see that the duct, before opening into the buccal cavity, opens into the vestibule, which becomes confluent with the lower part of the tooth sac. By such an arrangement it is made possible for the snake to inject a part of the secretion from the parotid gland into the severe wound at the time when it is being made by means of the sharp cutting-edge of the tooth.

Text-figures 12 & 13.



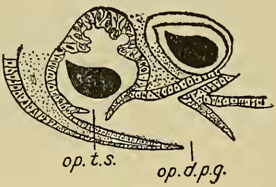


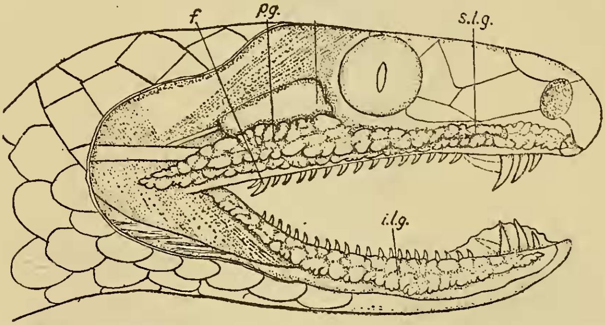
Fig. 12.—*Tropidonotus stolatus*. Tooth sac and fang. *t.s.* tooth sac; *f.* fang.

Fig. 13.—*Tropidonotus stolatus*. Longitudinal section of head in the region of the duct of the parotid gland, showing its opening into the buccal cavity. *op.t.s.* opening of duct into tooth sac; *op.d.p.g.* opening of duct of parotid gland. × 63.

LYCODON AULICUS.

Text-fig. 14 illustrates the general anatomy of the head dissected from the right side. The general survey will show that it is more advanced, and of a higher order than *Tropidonotus* in regard to its teeth and glands. The parotid gland (*p.g.*) in this snake is much enlarged, and its extension forward goes much further than in *Tropidonotus*, almost to the anterior end of the maxilla. Behind, it extends further than the angle of the jaw, and ends almost on a level with the superior labial gland; in fact, it has taken up so much of the glandular area that the superior labial gland is left reduced to a mere strip of glandular mass, which in dissection has an appearance more or less like that of the poisonous snakes. The lobules of the gland are larger than those of the superior labial gland. This is the only case I have yet met with in aglyphous or opisthoglyphous snakes where the poison gland is so highly developed and extends further forward than the middle of the eye. The most interesting feature to notice is the point of termination of the gland in front; it gradually narrows, and ends with a little bend above the enlarged fang-like tooth, apparently giving an impression in dissection of the duct of proteroglyphous snakes opening at the base of the fang. I hope at some future time, when more material is available, to make a more complete examination of the anterior end of the jaw of *Lycodon*, in order to put to the test Boulenger's suggestion of the probable evolution of the Proteroglypha from the Aglypha.

Text-figure 14.

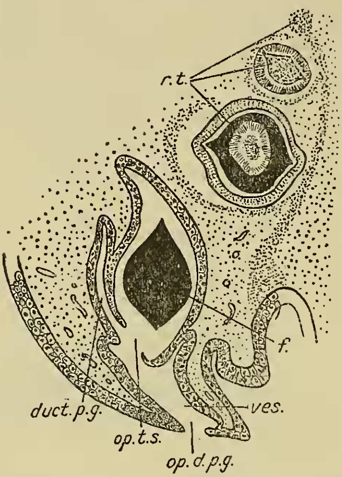


Lycodon aulicus. Dissection of head from the right side. Letters as before. × 6.

There are eighteen maxillary teeth, the anterior three are large and are followed by a diastema, the next fourteen are very small, and the last two are large and fang-like, and are enclosed within a muscular tooth sac similar to that already noted in *Tropidonotus*. In the transverse section (text-fig. 15) of the head of *Lycodon* will be seen the section of the posterior tooth sac (*f.* & *t.s.*). It will be noticed that the tooth is further specialised than that of *Tropidonotus* by the growth of cutting-edges on both sides. These cutting-edges give the appearance of a lancet.

The duct of the poison gland, like that of *Tropidonotus*, opens into the vestibule which communicates with the tooth sac at one end, and at the lower end opens into the buccal cavity (*op. d.p.g.*). A comparison of the course of this duct in *Tropidonotus* and *Lycodon* reveals the fact that in *Lycodon* the communication of the vestibule with the tooth sac is higher than in *Tropidonotus*, so that the secretion of the gland first fills the cavity of the tooth sac while on its course downwards into the buccal cavity. By such an arrangement of the duct the tooth-cavity is kept filled with the poison, and the tooth bathed in it. In this way a greater amount of poisonous fluid can be injected into the bigger wound, which is made by the two cutting-edges of the lancet-shaped tooth.

Text-figure 15.



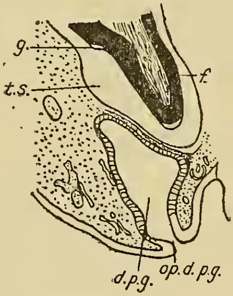
Lycodon aulicus. Transverse section of head in the region of the fang, duct of the poison gland and its opening into the tooth sac and the buccal cavity. *ves.* vestibule; other letters as before. × 63.

Opisthogylpha.

OXYBELIS FULGIDA.

This is a very interesting snake because of the fact that although it has acquired a better and surer means of injecting poison into the wound by developing a groove in the fang, it still retains the ancestral method of filling the tooth sac with the poison. West has described the anatomy of the head in detail, but for the present purpose of comparison his figures are insufficient. I have been unable to procure any specimens of *Oxybelis* to verify West's observation, and therefore cannot provide the necessary diagrams. So I have to base my arguments on West's account in the Proceedings of the Zoological Society, 1895. According to West, "the poison gland is very clearly defined and the superior labial gland is exceedingly long and narrow; it reaches to the anterior extremity of the maxilla, and consists of much smaller lobules than the poison gland. . . The maxilla possesses more teeth than that of any other snakes examined, there being twenty in one uninterrupted series. The first seventeen are equal in size and much curved; the posterior three are a little larger, compressed laterally, and the external face of each possesses a very shallow groove. The muscular folds surrounding these three posterior teeth are not united in front, and in consequence of a thin muscular fold across the base of the anterior grooved tooth the poison duct in this snake is placed in communication with the interior of the mouth before it is with the groove of the tooth." (See text-fig. 16.)

Text-figure 16.



Oxybelis fulgida. Transverse section of head in the region of the fang and the duct of the poison gland opening into the mouth (after West). *d.p.g.* duct of poison or parotid gland; *f.* fang; *g.* groove; *op.d.p.g.* opening of the duct of the parotid gland; *t.s.* tooth sac.

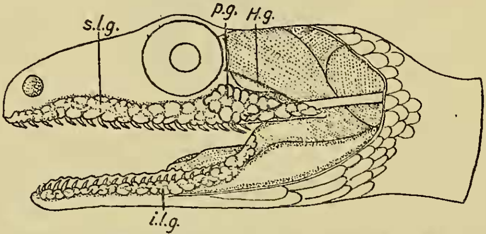
West has not given any figure of the dissection of the head, nor any section of the tooth (fang), but from the above description we may surmise from his use of the words "very clearly" that the parotid gland is even more highly differentiated in *Oxybelis* than in *Lycodon*. With regard to the fang, we may safely conclude from the above account of its lateral compression that it still retains some indication of cutting-edges on both sides like those of *Lycodon*, and at the same time has developed in "the external face . . . a very shallow groove." Referring now to the tooth-sac and the duct, I think that the thin muscular fold which West describes is the wall of what I have called the vestibule. Text-fig. 16 shows its connection with the buccal cavity, and probably if another series of sections were examined we should find the openings of the vestibule into the tooth sac. We can infer from this that the arrangement of the duct, vestibule, and tooth sac is more or less like that of *Lycodon*, and this is emphasized in his figure, which I reproduce.

Oxybelis, therefore, seems to be one of those types which connect the Aglypha with the Opisthoglypha. On the one hand it retains the aglyphous condition of the duct opening into the mouth, and on the other it has the characteristically opisthoglyphous grooved teeth.

CHRYSOPELEA ORNATA.

The general description of the glands and teeth has been given before (p. 304), but for comparison and discussion we will mention some of the facts again. On comparing the external appearance of the poison gland of *Chrysopelea* (text-fig. 17) with that of *Oxybelis*, described by West, and also with that of *Lycodon*, one is struck with the relative reduction in size; in fact, the gland is restricted to a very small area, and in shape and size resembles that of *Dendrophis*, which stands lowest in my series in the Aglypha (p. 307). In other words, it seems to be a case of retrogressive rather than of progressive evolution. But, on the other hand, it must be remembered that the snake has acquired more perfection by developing a deeper groove, by means of which it is confident of injecting a sufficient quantity of the poison into the wound, and that therefore it is obviously unnecessary to have a large gland and huge amount of secretion.

Text-figure 17.



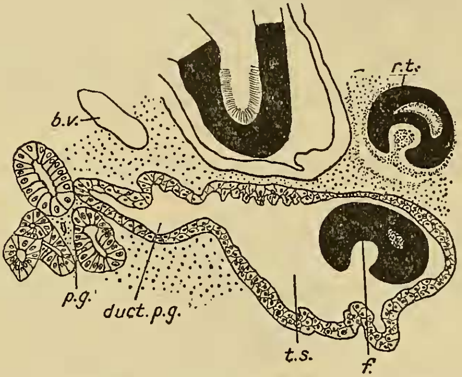
Chrysopelea ornata. Dissection of head from the left side. *H.g.* Harderian gland; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *s.l.g.* superior labial gland. × 3.

It also will be seen that the secretion coming from the gland passes directly into the tooth sac, where greater use can be made of it than if it were squandered in the buccal cavity.

Now, if we examine the transverse section of *Chrysopelea* (text-fig. 18) and compare it with that of *Oxybelis* (text-fig. 16), we find the former specimen is more advanced in many ways. The fang has lost the remains of the cutting-edges on both sides, but has developed a deeper groove than that in the fang of *Oxybelis*.

Regarding the duct, it no longer opens into the vestibule, but directly into the tooth sac. The opening of the vestibule into the mouth cavity is closed, and the tooth sac becomes comparatively bigger. If in text-fig. 16 the opening of the vestibule into the mouth is closed, and at the same time the thin membrane, to which West refers and which is also shown in text-fig. 15, atrophies so that the cavities of the vestibule and tooth sac are confluent with one another, the condition, as shown in text-fig. 18 of *Chrysopelea*, is arrived at. I have shown that the two cavities really become confluent in *Tropidonotus* and *Lycodon* near to the opening into the mouth. The evidence in favour of the theory that such changes have been brought about is shown by the fact that the duct in *Chrysopelea* opens, not into the mouth, but into the middle of the tooth sac.

Text-figure 18.



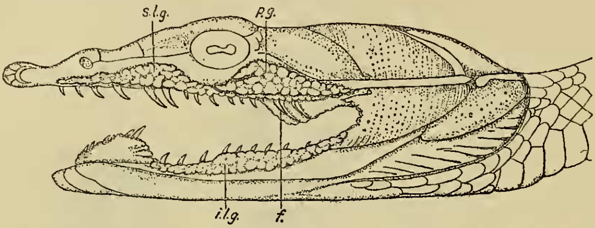
Chrysopelea ornata. Transverse section of the head in the region of the poison gland, its ducts, the tooth sac, and the fang. *b.v.* blood-vessel; *duct.p.g.* duct of the poison gland; *f.* fang; *p.g.* poison or parotid gland; *r.t.* reserve tooth; *t.s.* tooth sac. × 63.

In conclusion, then, we see that *Chrysopelea* is higher in grade than *Oxybelis*, for the reason that the duct of the poison gland opens directly into the tooth sac and that there is a deeper groove in the fang.

DRYOPHIS MYCTERIZANS.

This snake is in many respects much more advanced than *Chrysopelea*. The parotid gland is more highly developed, and has become a distinct organ, though it still remains embedded in the superior labial gland. At the same time, the secretion of the gland becomes more poisonous; it has been proved that the bite of this snake is fatal to small animals (West). The fangs (text-fig. 19) have shifted a little forward in the jaw, and are therefore in a less concealed position, being rendered capable of inflicting a more severe wound. There are only fourteen teeth in the maxilla: this reduction may possibly be explained by the fact that the teeth, which are present, are large, strong, and more exposed, and better able to kill the prey or to paralyse it quickly with the poison that is now injected directly into the puncture made by the fang.

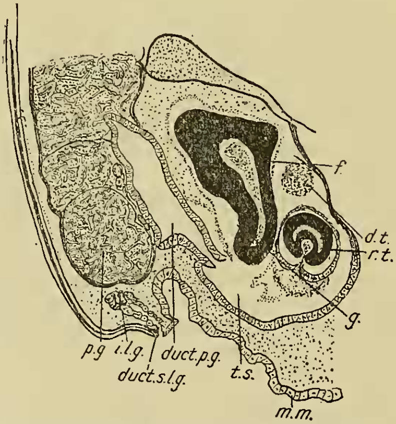
Text-figure 19.



Dryophis mycterizans. Dissection of the head from the left side. × 3. Letters as before.

In the transverse section (text-fig. 20) we notice that the duct of the poison gland has shifted still further up than in *Chrysopelea* (text-fig. 18), so that its opening into the tooth sac is nearer to the base of the tooth and close to the beginning of the groove. The poison coming from the gland passes directly into the groove. In *Dryophis* the groove is now more or less in the shape of a canal, as the edges are almost in contact.

Text-figure 20.



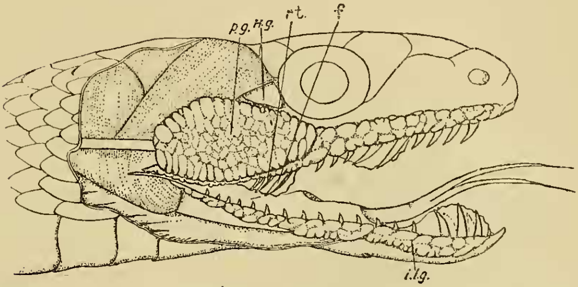
Dryophis mycterizans. Transverse section of the head in the region of the parotid and superior labial gland and their ducts, the tooth sac and the fang. *m.m.* mucous membrane; other letters as before. × 63.

PSAMMOPHIS SIBILANS.

This is one of the most highly-developed of the opisthoglyphous snakes. The very appearance of text-fig. 21 will reveal the fact that it is more ferocious and is capable of doing more harm than *Dryophis*. The structure of the teeth and gland positively prove that it is so, and this is emphasized in the description in the first part of this paper.

Looking at the poison gland, one finds that it has assumed a distinct and definite shape, quite separate from the superior labial gland. The poison fang has moved still further forward in the buccal cavity than in *Dryophis*. It is straighter, and it lies directly below the eye. The shape of the poison fang is of importance, *i. e.* being straight and not bent backward. The fang that is bent backward at an angle is of more use in inflicting a wound on prey that is already in the mouth, while a straight tooth is of greater use as a weapon of offence and defence, as it can inflict a wound on prey that is outside the mouth. Another improvement has taken place; the groove has become deeper, and extends through the whole length of the tooth, ending at the very tip. It has also shifted from the side of the tooth to the front, in order to be still nearer the opening of the duct, which opens in front of the tooth sac as in the highly-developed poisonous snakes.

Text-figure 21.



Psammophis sibilans. Dissection of head from the right side. *f.* fang; *H.g.* Harderian gland; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *r.t.* reserve tooth. × 3.

It is unfortunate that I have not been able to examine sections of this genus to see the connection of duct with the teeth; but I have seen only one specimen, and it was kindly lent to me by Miss Procter, of the British Museum, for purposes of observation but not for sectioning.

Conclusions.

Taking a general view of this series, it is interesting to endeavour to explain the factors which have brought about the gradual change and complicated modifications leading us to the most highly-developed snakes.

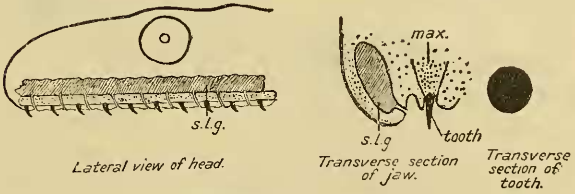
Our hypothetical ancestor of the Aglypha would in all probability be one in which the teeth were equal and peg-like, while the superior labial gland showed no differentiation. The secretion was used more or less for digestive purposes, like the saliva of other animals. The next step in evolution was brought about by the necessity of having a stronger secretion which would have the action of disintegrating the prey more quickly within the mouth. A portion of the gland in the region of the maxilla was differentiated to perform this function. The tooth nearest to the opening of the duct of this gland became a little different from the others by acquiring a cutting-edge, and the duct of this portion moved nearer to it. By this arrangement it became possible for the snake to make a deeper and larger scratch and to pour poison on the wound, as in the case of *Dendrophis*. However, by this method the poison from the now differentiated poison gland is inevitably mixed, and therefore diluted with the general saliva in the mouth. In order to avoid this dilution, the tooth nearest to the opening of the poison gland became bigger and separated from the rest by being enclosed in a special sac. The sac is kept filled with poison, so that the tooth is always immersed in it (*Lycodon* and *Tropidonotus*). This arrangement acted as a sure means of making a deeper wound, which may be compared to poisoning the prey by probing the body with a lancet besmeared with poison. This is undoubtedly a slow process, as a sufficient quantity of poison could not be injected.

The next step is a great improvement in the tooth—a groove appeared which became almost a canal, as we have seen in *Chrysopelea* and *Dryophis*. At the same time, the gland became a distinct organ (text-fig. 21) from the general glandular mass of the superior labial gland, and the duct moved upward to open finally at the base of the tooth. Evidently this is a great advance, for by this means pure unmixed poison can be injected into the deeper tissue. We may compare this with the modern method of injection by a hypodermic or intermuscular syringe, which acted almost instantaneously. This seems to be the origin of the opisthoglyphous snakes.

But even this method has its defects in some ways. The grooved tooth being situated far behind, the prey has to be taken well into the mouth before the operation can be performed. Besides, this tooth cannot be utilised as an organ of offence and defence. *Dryophis*, in a primitive manner, has overcome this difficulty by developing an extra solid tooth in the anterior end of the jaw (text-fig. 20) which disables the prey before it is carried further into the mouth to the region of the poison fang. In order to do away with unnecessary apparatus and provide one fang which would serve all purposes, the poison fang has shifted forward right to the front of the mouth, dragging with it the duct of the poison gland. This gave rise to vipers, where we know that the poison apparatus is perfect in all ways and that the other teeth have disappeared. Probably evolution has taken place in this way, as already pointed out by Boulenger: "the series (in Opisthoglypha) culminating in such forms as have the maxillary bone much abbreviated, the solid teeth reduced to two or three, and the fang extremely large and deeply grooved. If we turn to the skull of the least specialised among the Viperidæ, we see that the poison fangs are situated on the posterior extremity of the maxillary bone, close to its articulation with the ectopterygoid, a condition which is identical with that of Opisthoglyphous Colubrids. It is therefore clear to me that the Viperids have been derived from the Opisthoglyphs."

Summary.

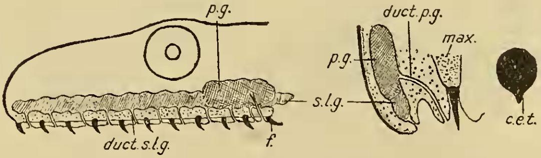
Text-figure 22.



1. Hypothetical ancestor.

Gland in the region of maxilla undifferentiated: teeth all equal and peg-like. All the ducts open in the buccal cavity far away from teeth.

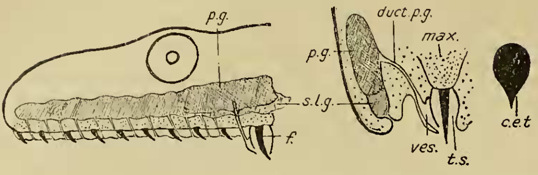
Text-figure 23.



2. *Dendrophis pictus.*

A small portion, near the posterior end, of the gland (*p.g.*) differentiated. The duct of this portion moved inward to open near the hinder tooth (*f*). The latter has become different from others by being more bent inwards, and also has developed a slight cutting-edge (*c.e.t.*) on the inner side.

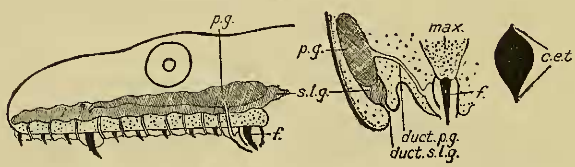
Text-figure 24.



3. *Tropidonotus stolatus.*

A greater portion of the gland in the region of the maxilla is differentiated to form the parotid or poison gland (*p.g.*). The hinder tooth (*f*) is much bigger than those in front. The cutting-edge (*c.e.*) is more marked. It is also enclosed within a special sac (*t.s.*). The duct of parotid glands (*duct p.g.*) enlarges at the end to form a cavity (*ves.*) which becomes confluent with the tooth sac before opening into the mouth. Sac is kept filled with the secretion and the tooth dipped into it.

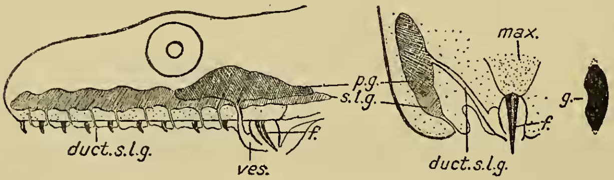
Text-figure 25.



4. *Lycodon aulicus.*

The parotid gland is much enlarged, and almost extends up to $\frac{3}{4}$ of maxilla. The duct (*duct p.g.*) is similar to *Tropidonotus*, except that it opens a little higher. The tooth is like a lancet, with a cutting-edge on each side.

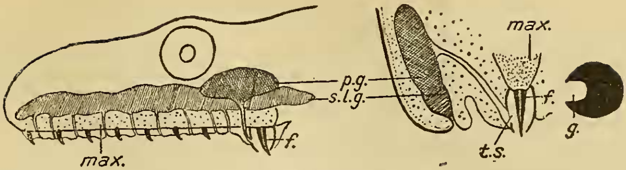
Text-figure 26.



5. *Oxybelis fulgida.*

The poison gland (*p.g.*) well developed. The arrangement of the duct is similar to that of *Lycodon* and *Tropidonotus, i. e.* enlarges to form vestibule (*ves.*) before opening into the mouth (Aglyphous condition). The fang (*f*) is laterally compressed. Has almost lost cutting-edges, but has acquired a very shallow groove like Opisthoglypha.

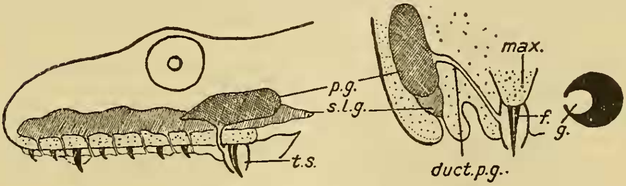
Text-figure 27.



6. *Chrysopelea ornata.*

The poison gland is reduced in size, due to the fact that the fang (*f*) has acquired a deeper groove (*g*), through which a greater amount of secretion can be injected into the wound, and there is very little waste. The wall between the vestibule (*ves.*) and the tooth sac has disappeared; at the same time the opening of the duct into the mouth cavity is closed, and hence the duct (*p.g.*) opens directly into the tooth sac.

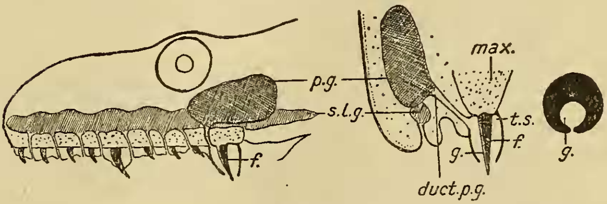
Text-figure 28.



7. *Dryophis mycterizans.*

The poison gland (*p.g.*) is much more differentiated. The groove (*g.*) of the fang is deeper and almost like a canal. The duct (*duct p.g.*) has shifted upward to open into the tooth sac almost near to the base of the fang, which has also moved forward in the mouth cavity.

Text-figure 29.



8. *Psammophis sibilans.*

The poison gland (*p.g.*) is distinct—almost a separate organ. The fang (*f*) is almost straight, and has shifted still further in the mouth cavity. The groove lies in front of the tooth instead of on the side, nearer to the beginning of the groove.

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